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Unravelling a biogeographical knot: origin of the 'leapfrog' distribution pattern of Australo-Papuan sooty owls (Strigiformes) and logrunners (Passeriformes)

J. A. Norman[1], L. Christidis[1*], L. Joseph[2], B. Slikas[3] and D. Alpers[2]

[1]*Sciences Department, Museum Victoria, GPO Box 666E, Melbourne, Victoria 3001, Australia*
[2]*Department of Ornithology, Academy of Natural Sciences of Philadelphia, 1900 Benjamin Franklin Parkway, Philadelphia, PA 19103-1195, USA*
[3]*Department of Zoological Research, National Zoological Park, Smithsonian Institution, Washington, DC 20008-2598, USA*

Molecular analysis of two Australo-Papuan rainforest birds exhibiting correlated 'leapfrog' patterns were used to elucidate the evolutionary origin of this unusual pattern of geographical differentiation. In both sooty owls (*Tyto*) and logrunners (*Orthonyx*), phenotypically similar populations occupy widely disjunct areas (central-eastern Australia and upland New Guinea) with a third, highly distinctive population, occurring between them in northeastern Queensland. Two mechanisms have been proposed to explain the origin of leapfrog patterns in avian distributions: recent shared ancestry of terminal populations and unequal rates or phenotypic change among populations. As the former should generate correlated patterns of phenotypic and genetic differentiation, we tested for a sister relationship between populations from New Guinea and central-eastern Australia using nuclear and mitochondrial DNA sequences. The resulting phylogenies not only refute recent ancestry as an explanation for the leapfrog pattern, but provide evidence of vastly different spatio-temporal histories for sooty owls and logrunners within the Australo-Papuan rainforests. This incongruence indicates that the evolutionary processes responsible for generating leapfrog patterns in these co-distributed taxa are complex, possibly involving a combination of selection and drift in sooty owls and convergence or retention of ancestral characteristics in logrunners.

Keywords: leapfrog; comparative phylogeography; speciation; mitochondrial DNA; Aves; systematics

1. INTRODUCTION

Within the rainforests of eastern Australia and New Guinea, leapfrog patterns of distribution have been reported for several avian species complexes including sooty owls *Tyto*, logrunners *Orthonyx* and ground-thrushes *Zoothera* (Schodde & Calaby 1972; Schodde & Mason 1981; Ford 1983). In each case, similar but geographically disjunct populations are separated by an intervening population that is phenotypically distinct. This striking pattern of geographical variation appears to be relatively common among montane forest birds, particularly those of the humid Andean forests (Remsen 1984).

Hypotheses to explain the origin of leapfrog distributions (summarized in Remsen (1984)) can be divided into two groups. In one, phenotypic similarity of terminal populations is due to their more recent common ancestry with long-distance dispersal or vicariance invoked to explain the evolution of their disjunct distributions. The dispersal hypothesis assumes that one of the terminal populations was colonized through long-distance dispersal from the other. Diamond (1973) proposed such a mechanism for birds in montane New Guinea in which competitive exclusion among adjacent populations led to the dispersing taxa colonizing more distant sites. Under the vicariance hypothesis, it is assumed that the terminal populations were once connected by a habitat corridor that by-passed the central population. Subsequent vicariance events presumably led to the isolation of the terminal populations. The second group of hypotheses posits that the leapfrog pattern results from unequal rates of phenotypic change among populations. This could arise through environmentally determined selective pressures leading to convergent or parallel evolution in the terminal populations or to rapid divergent evolution in the central population. It has also been suggested that variation in rates of phenotypic change among populations could arise through stochastic processes such as drift (Remsen 1984).

Remsen (1984) concluded that leapfrogging in Andean birds was the result of random phenotypic change, but distinguishing between the hypotheses is difficult and it remains unclear whether leapfrog patterns observed in diverse taxa have similar origins. A first step towards clarifying the evolutionary origin of leapfrog patterns is to determine whether the populations exhibit concordant patterns of phenotypic and genetic differentiation. Concordant patterns, in which the terminal populations are identified as sister taxa, are predicted where the leapfrog distribution is generated by long-distance dispersal events or historical biogeographical connections. In both cases, the leapfrog pattern in phenotype accurately reflects the sequence of evolutionary relationships among populations. Discordant patterns, however, are predicted where

* Author for correspondence (lchrist@museum.vic.gov.au).

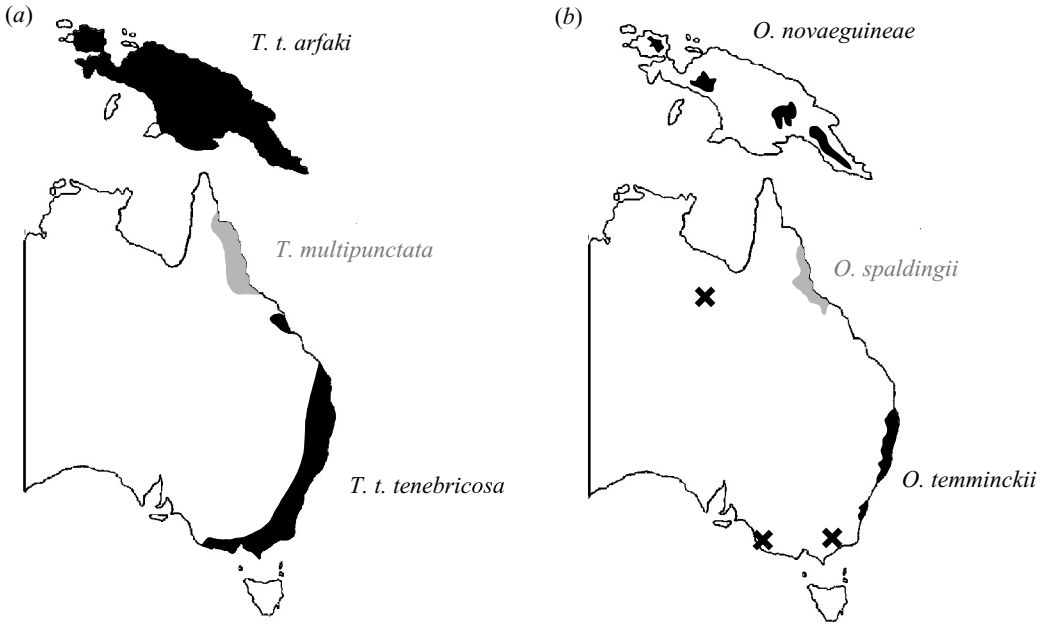

Figure 1. Geographical distribution of (*a*) sooty owls *Tyto* and (*b*) logrunners *Orthonyx* in Australo-Papuan rainforests. The distribution of the New Guinean logrunner is uncertain, but it occurs within each of the regions indicated. Species names and distributions for both groups are shaded to emphasize the leapfrog pattern, with the phenotypically similar terminal populations indicated in black. Crosses indicate the location of fossil sites for logrunners in northern (Riversleigh, Queensland) and southern (Green Waterhole Cave, South Australia and Pyramids Cave, Victoria) Australia.

stochastic (drift) or deterministic (selection) processes have resulted in unequal rates of phenotypic evolution. In each of these cases, a sister relationship is predicted between adjacent, but phenotypically distinct, populations.

Here, we use phylogenetic methods to investigate the origin of leapfrog patterns in two avian species complexes inhabiting the tropical and subtropical forests of New Guinea and eastern Australia: the sooty owls (Strigiformes: *Tyto*) and logrunners (Passeriformes: *Orthonyx*). Members of both species complexes show correlated distributional patterns with disjunct populations occurring in upland New Guinea, the wet tropics of northeast Queensland and the subtropical rainforests of central-eastern Australia (figure 1). In both complexes, the central population from northeast Queensland is phenotypically the most distinct and treated as a separate species in current classifications (Christidis & Boles 1994; Schodde & Mason 1999). A recent morphological and molecular study of the New Guinean logrunner (Joseph *et al.* 2001) revealed greater than expected levels of divergence within this complex, leading to recognition of the New Guinean population as a distinct species. The present study extends these analyses by the inclusion of additional mitochondrial DNA (mtDNA) and nuclear DNA (nucDNA) data, and uses comparative phylogeography to test for common historical biogeographical influences on the evolution of the leapfrog pattern in two unrelated but essentially co-distributed species complexes. We use the new dataset to: (i) derive phylogenetic relationships among Australian and New Guinean taxa of sooty owls and logrunners; (ii) measure DNA-level divergences among taxa in each complex; (iii) reassess their systematics and historical biogeography; and (iv) explain the origin of their leapfrog distribution patterns.

2. MATERIAL AND METHODS

(a) *Taxomomy, morphology and specimens*

Current taxonomy defines populations of sooty owls from New Guinea (*Tyto tenebricosa arfaki*) and central-eastern Australia (*T. t. tenebricosa*) as subspecifically distinct with the intervening population from northeast Queensland a separate species, *T. multipunctata* (Schodde & Mason 1981, 1999). *Tyto multipunctata* is readily distinguished by its smaller size, lighter coloration, presence of larger spotting in the plumage and absence of sexual dimorphism in the size of the feet and bill (Schodde & Mason 1981). Although populations of logrunners from New Guinea and central-eastern Australia have traditionally been treated as conspecific, recent molecular and morphological analyses indicate that they are better treated as distinct species, *Orthonyx novaeguineae* and *O. temminckii* (Joseph *et al.* 2001). The intervening population from northeast Queensland is also assigned to a separate species *O. spaldingii* (Schodde &

Mason 1999). Logrunners from New Guinea and central-eastern Australia are similar in size and plumage (mottled underparts, barred wings, grey bellies), whereas *O. spaldingii* is larger and darker with plain underparts, a coloured ring of ocular skin (Joseph *et al.* 2001) and very different vocalizations (McGuire 1996). For simiplicity, we use the vernacular group names 'sooty owls' and 'logrunners' throughout, and refer to individual taxa with scientific names.

Our primary dataset consisted of DNA sequences from three mitochondrial genes (cytochrome *b*, ND2 and ATPase 8) and a nuclear intron (fibrinogen intron V or myoglobin intron II) for three sooty owls and seven logrunners. Tissue samples for these 10 individuals were obtained from Museum Victoria (MV), South Australian Museum (SAM) and the Australian National Wildlife Collection (ANWC). Specimen details (museum, sample code, locality) are: *T. t. arfaki* (SAM, B22, Waro, Southern Highlands Province, Papua New Guinea); *T. t. tenebricosa* (ANWC, 47350, Newcastle, New South Wales, Australia); *T. multipunctata* (MV, C687, Mt Lewis, Queensland, Australia); *O. novaeguineae* (MV, E420, Gulugawa Ridge, Gulf Province, Papua New Guinea); *O. temminckii* (MV, B831 and B842, Cambridge Plateau, New South Wales, Australia); *O. spaldingii* (MV, F247 and F257, Atherton Tableland, Queensland, Australia; MV, C699 and C701, Mt Lewis, Queensland, Australia). The grass owl *T. capensis* (MV Tlongi.1, Nanima, New South Wales, Australia) and grey-crowned babbler *Pomatostomus temporalis* (MV, D257, Alice Springs, Northern Territory, Australia) were included as outgroups.

To ensure adequate sampling of intra-taxon variation, cytochrome *b* and ATPase 8 sequences were also obtained from a further five sooty owls: *T. t. arfaki* (ANWC 4529, 9159, 47122), *T. t. tenebricosa* (ANWC 47077) and *T. multipuntata* (ANWC 28680). This included ancient DNA obtained from museum skins analysed at the Smithsonian National Zoological Park and Academy of Natural Sciences, Philadelphia, using the methods described in Joseph *et al.* (1999). Additional cytochrome *b* and ATPase 8 sequences from eight logrunners (six *O. novaeguineae* and single representatives of *O. temminckii* and *O. spaldingii*) were obtained from Joseph *et al.* (2001). Using this approach, we examined a total of 23 individuals with a minimum of two individuals per taxon sampled from each of the three rainforest blocks (New Guinea, northeast Queensland and central-eastern Australia).

(b) *DNA extraction, amplification and sequencing*

Primers for PCR amplification and sequencing were: cytochrome *b*, L14841 and H15149 (modified from Kocher *et al.* 1989); ATPase 8, L8929, H9240, L9051 and H9241 (developed by G. Seutin and E. Bermingham); ND2, pND2-L (Ericson *et al.* 2002) and ND2-2 (H6315 in Kirchman *et al.* (2001)); fibrinogen intron V (developed at the Field Museum of Natural History, Chicago, IL, USA); myoglobin intron II, Myo2 and Myo3f (Heslewood *et al.* 1998). The following internal sequencing primers were also used: NS2 and NS3a (Norman *et al.* 1998) for ND2 of sooty owls; amyND2int.nc1 (5′TCAAAAGTGGAATGGGGCTA) and HEND2int.c (Ericson *et al.* 2002) for ND2 of logrunners; Myoint.c and Myoint.nc (Heslewood *et al.* 1998) for the myoglobin intron of logrunners. Protocols for DNA extraction, amplification and sequencing were essentially as described in Norman *et al.* (1998), Joseph *et al.* (1999) and Ericson *et al.* (2002).

(c) *Sequence analyses*

Sequences for each fragment were edited and aligned by eye. PAUP* 4.0b8 (Swofford 1998) was used to calculate sequence divergences and to perform phylogenetic analyses for: (i) individual genes or regions; (ii) the combined mtDNA sequences; and (iii) the total data (mtDNA plus nuclear intron sequences). Maximum-parsimony (MP) analyses were conducted using global search options and random addition of taxa. Neighbour-joining (NJ) (Saitou & Nei 1987) trees were constructed using the Kimura two-parameter (Kimura 1980) and Tajima–Nei (Tajima & Nei 1984) distance options. Trees were also derived with maximum-likelihood (ML) estimates with global search options under the HKY model (Hasegawa *et al.* 1985). Significance of branching points were assessed with the conventional non-parametric bootstrap (1000 pseudoreplicates). Spectral analyses (Hendy & Penny 1993) were also conducted to permit consideration of the sequence data independently of the phylogenetic trees. This analysis employed the program SPECTRUM 2.0 (Charleston 1998). Branching patterns were also explored from four taxon statements using Lake's (1987) invariants and quartet puzzling as implemented in PAUP* 4.0b8 (Swofford 1998). The molecular clock hypothesis of constant evolutionary rates among lineages was tested using BINHALF (Mindell & Honeycutt 1990) and the method of Muse & Weir (1992). The tests were performed individually for each gene or region, the combined mtDNA data and the total data for both species complexes. The mtDNA data were also used to test for constant evolutionary rate between sooty owls and logrunners using the chicken (Desjardins & Morais 1990) as an outgroup.

3. RESULTS

A total of 1215 bp of mtDNA sequence was obtained for the three sooty owls and seven logrunners included in the primary dataset (i.e. specimens sequenced for the complete complement of genes). This comprised 717 bp of ND2, 300 bp of cytochrome *b* and 198 bp of ATPase 8. In addition, 691 bp of the nuclear fibrinogen intron V was obtained for the sooty owls, and 720 bp of the nuclear myoglobin intron II obtained for the logrunners. Partial sequence data (498 bp of cytochrome *b* and ATPase 8) were also obtained for an additional five sooty owls. Representative sequences have been lodged in GenBank (accession numbers AY148033–AY148070, AY148951–AY148953, AY064728 and AY064730.).

Intra-taxon variability, assessed using combined cytochrome *b* and ATPase 8 sequences, was negligible in sooty owls (0–0.2%) and ranged from 0.2% to 7.2% in logrunners. The highest values were between individuals of *O. novaeguineae* sampled from different localities in New Guinea. This reflects previous findings and taxonomy with subspecific status recognized for the forms in western (*O. n. novaeguineae*), central (*O. n. dorsalis*) and eastern New Guinea (*O. n. victoriana*) (Joseph *et al.* 2001). As sequences within populations formed monophyletic assemblages, single individuals were considered to be representative of the populations in subsequent phylogenetic analyses. Kimura two-parameter estimates of sequence divergence among populations for both the combined mtDNA and nDNA sequences are presented in table 1. Levels of mtDNA divergence among logrunners (15.6–18.1%) were over an order of magnitude greater than

Table 1. Kimura two-parameter distances between populations of (*a*) sooty owls (*Tyto*) and (*b*) logrunners (*Orthonyx*) from New Guinea (NG), central-eastern Australia (ceAUS) and northeastern Queensland (neQLD). Mitochondrial DNA divergences are below the diagonals, nuclear DNA divergences are above.

	NG	ceAUS	neQLD
(*a*)			
Tyto tenebricosa arfaki (NG)	—	0.004	0.002
Tyto tenebricosa tenebricosa (ceAUS)	0.006	—	0.003
Tyto multipunctata (neQLD)	0.008	0.007	—
(*b*)			
Orthonyx novaeguineae (NG)	—	0.008	0.003
Orthonyx temminckii (ceAUS)	0.181	—	0.011
Orthonyx spaldingii (neQLD)	0.156	0.180	—

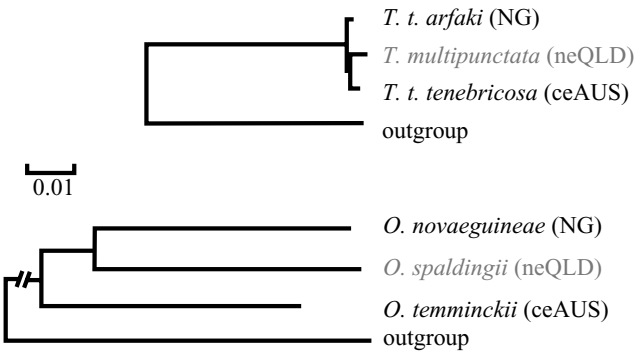

Figure 2. Phylogenetic relationships among sooty owls and logrunners inferred from mtDNA sequence data. Trees are drawn to the same scale and constructed using the NJ method. Species names are shaded as in figure 1. Abbreviations for geographical locations occupied by each taxon are included in brackets. (NG, New Guinea; ceAUS, central-eastern Australia; neQLD, northeastern Queensland.)

observed in the myoglobin intron II sequences (table 1*a*) and the mtDNA sequences of sooty owls (table 1*b*).

Prior to conducting phylogenetic analyses the data were assessed for evidence of rate heterogeneity that could lead to spurious relationships being reconstructed. No evidence of significant rate variation was found for the total, combined mtDNA or single gene datasets for either species complex ($p > 0.05$ in all tests). However, there was a trend towards decreasing rates of evolution at higher latitudes in the ND2, cytochrome *b* and ATPase 8 genes of logrunners, with the central-eastern Australian population *O. temminckii* accumulating the smallest number of mutations. This pattern was not evident in the myoglobin intron II sequences. Although no tests were statistically significant, we note that their sensitivity may be compromised by the use of divergent outgroups (Wu & Li 1985). Despite the level of mtDNA divergence within the logrunners being an order of magnitude greater than the sooty owls (table 1), there was no evidence of significant heterogeneity in the rate of sequence evolution between these taxa (tests performed using a sooty owl and a logrunner with a chicken as the outgroup).

Within the sooty owl complex there were too few parsimony informative sites in either the mtDNA or nuclear fibrinogen intron V sequences to make MP or ML analyses feasible. Representatives of all three sooty owl populations were similarly divergent from one another in mtDNA (0.60–0.80%) and nDNA (0.20–0.40%) (table 1*b*). The NJ tree based on the combined mtDNA sequences (figure 2) identified central-eastern Australian *T. t. tenebricosa* and northeastern Queensland *T. multipunctata* as sister taxa (with no bootstrap support) as did Lake's invariants. Relationships could not be resolved by the quartet puzzling method. Although the NJ tree based on nDNA sequences identified a sister relationship between *T. t. tenebricosa* and New Guinean *T. t. arfaki*, the latter was closest to *T. multipunctata* in terms of genetic distance. Thus, no clear pattern of sister relationships could be identified within sooty owls.

MP analysis of the total mtDNA sequences identified *O. spaldingii* from northeastern Queensland and *O. novaeguineae* from New Guinea as sister taxa in the shortest tree (146 steps) with bootstrap support of 71%. The tree in which phenotypically similar populations *O. novaeguineae* and *O. temminckii* were constrained as sister taxa was 12 steps longer. ML with and without a molecular clock also identified *O. spaldingii* and *O. novaeguineae* as sister taxa, as did the NJ tree (figure 2) (79% bootstrap support) and quartet puzzling. The latter test was performed using alternative subspecies of *O. spaldingii* with similar results. Spectral analysis provided the most support (0.014) and least conflict (0.074) for this relationship, while the two alternative relationships had much lower support (0.005 and –0.005) and more conflict (0.189 and 0.262). A sister relationship between *O. spaldingii* and *O. novaeguineae* was also supported by Lake's method of phylogenetic invariants ($p = 1.000$, as opposed to 0.250 and 0.723 for other relationships). In both the Spectral and Lake's analyses, a sister relationship between the phenotypically similar populations *O. novaeguineae* and *O. temminckii* received least support. There was limited variation in the nuclear myoglobin intron II (only eight out of 720 sites varied) so MP and ML analyses were not possible. Nevertheless, divergence was lowest between *O. spaldingii* and *O. novaeguineae* (table 1*a*), and this relationship was identified by NJ analysis.

4. DISCUSSION

Our results allow an analysis of the biogeographical history and phylogenetic relationships of taxa within the sooty owl and logrunner complexes, as well as an assessment of the evolutionary origin of the leapfrog pattern in these Australo-Papuan rainforest birds.

(a) *Systematics and phylogeny*

Low levels of sequence divergence among sooty owls raise doubts about the current circumscription of the complex into two species. All three taxa were similarly divergent from one another in both the mitochondrial (0.60–0.80%) and nuclear (0.20–0.40%) DNA sequences (table 1*b*). Comparison with cytochrome *b* or ND2 sequences of strigid owls indicates that these estimates are an order of magnitude lower than typically observed among owl species. Examples include: 9.0–12.0% in the *Strix aluco–butleri–woodfordii* complex (Heidrich & Wink

1994); 6.3–8.8% in the *Otus atricapillus* complex (Heidrich *et al.* 1995); and 5.4% in the *Ninox rufa–strenua* complex (Norman *et al.* 1998). Levels observed among sooty owls are comparable with subspecific differentiation within the Boobook owl *Ninox novaeseelandiae* (1.5–2.3%) (Norman *et al.* 1998) and in birds generally (Avise & Walker 1998). Consequently, the complex is best treated as a single species, *T. tenebricosa*, as was the case prior to the revision of Schodde & Mason (1981).

For logrunners, analysis of a more comprehensive dataset supports Joseph *et al.* (2001) in finding that phenotypically similar populations from New Guinea and central-eastern Australia are distinct species *O. novaeguineae* and *O. temminckii*, respectively. MtDNA sequences of these taxa were as divergent from each other (18.1%) as they were from *O. spaldingii* (15.6–18.0%). Moreover, this level of divergence was greater than that previously recorded between subspecies of *O. spaldingii* (2.6%) and *O. novaguineae* (up to 7.2%) (Joseph *et al.* 2001). Although limited variation was found in the nuclear myoglobin intron II sequences, the data clearly support the recognition of three logrunner lineages. Similarities in these independent estimates of logrunner phylogeny indicate that species and gene trees are concordant.

The phylogenetic relationships and depths of divergences identified here illustrate that rates of molecular and morphological evolution are decoupled in both the logrunner and sooty owl complexes. This is a common phenomenon in molecular phylogenetic studies of birds (e.g. Omland *et al.* 2000) and cautions against the exclusive use of phenotypic characters when making taxonomic assessments.

(b) *Historical biogeography: integrating molecules, fossils and ecology*

A particularly striking feature of the sooty owl and logrunner phylogenies is the markedly different depths of the lineages. As these differences are not due to variation in the rate of DNA evolution, the occurrence of deep divergences among logrunners indicates that they are a considerably more ancient radiation than sooty owls. This is consistent with the fossil record for both species complexes. Miocene logrunner fossils have been recovered from sites in northern and southern Australia (figure 1) (Baird 1985, 1993; Boles 1993), whereas no pre-Quaternary fossil tytonids are known from this region (Rich 1991). That the logrunners are an old endemic lineage is also supported by protein allozyme data (Christidis 1991; Christidis & Schodde 1991) and nDNA and mtDNA sequences (Ericson *et al.* 2002), which identify logrunners as part of an early Australo-Papuan passerine radiation. This, coupled with the widespread locations at which logrunner fossils have been found in eastern Australia (Baird 1985; Boles 1993), indicate that the current disjunct distribution of the three species is a result of their isolation and subsequent divergence in response to the retraction in range of the Australo-Papuan rainforests since the mid-Miocene. The sooty owls, as members of a cosmopolitan genus with a restricted fossil history in the region, are likely to be more recent arrivals into the Australo-Papuan rainforest avifauna.

Consideration of habitat also adds an important ecological dimension to any attempt to explain the contrasting histories of these two species complexes. Although occupying broadly similar ranges centred on Australo-Papuan rainforests, sooty owls are found in a wider range of habitats than logrunners. In each of the three regions, the range of sooty owls extends beyond the rainforest and into adjacent wet schlerophyll, eucalypt-dominated habitats (Schodde & Mason 1981, 1997), whereas logrunners are strict rainforest specialists (Joseph *et al.* 2001). The wider habitat tolerance of sooty owls has probably been an important factor in preventing significant evolutionary divergence among populations. This may have acted to limit the impact of Plio-Pleistocene habitat fragmentation through greater historical connectivity and gene flow among populations or provided avenues for recent dispersal into already fragmented habitats.

(c) *Origin of the leapfrog pattern*

The absence of clear evidence for a sister relationship between phenotypically similar populations in both species complexes enables us to unequivocally reject more recent common ancestry of terminal populations in favour of unequal rates of phenotypic evolution as an explanation for the leapfrog pattern in sooty owls and logrunners. Both stochastic and deterministic processes have been implicated as possible mechanisms underlying unequal rates of phenotypic evolution in birds. Remsen (1984) considered stochastic processes (the chance accumulation of mutations) to be the most likely explanation for the origin of the leapfrog pattern in Andean birds. This interpretation was based on the observed lack of geographical concordance in the position of the central populations of the taxa studied and the presumption that geographically concordant patterns would occur in the presence of strong environmental pressures. This is further supported by the observation that plumage coloration in birds is often under simple genetic control (Cooke & Buckley 1987). At the molecular level, single point mutations (Theron *et al.* 2001) and short deletions (Tobita-Teramoto *et al.* 2000) in genes involved in melanin biosynthesis have been linked with avian plumage polymorphisms. Consequently, the phenotypic differences that underlie leapfrog patterns may be the result of only one or a few mutations.

Several lines of evidence indicate that the origin of the leapfrog pattern in Australo-Papuan rainforest birds is more complicated, involving a combination of both stochastic and deterministic processes. Within the recently evolved sooty owl complex, diagnostic phenotypic characters of the central population (paler more intensely spotted plumage) could result from few mutations that have become fixed, by chance, over a short period. A similar explanation has been proposed for the Rufous-naped brush-finch *Atlapetes rufinucha* complex, in which different levels of pigment deposition are believed to produce a leapfrog pattern involving grey and yellow forms (Remsen & Graves 1995). Selection may also have played a part in shaping the distinctive morphology of the central population of sooty owls, particularly its small size and lack of sexual dimorphism. This population is the most geographically restricted and almost exclusively inhabits dense wet forests where small size would be an advantage (Schodde & Mason 1981). Likewise, the absence of sexual dimorphism in the feet and bill is consistent with a role of selection, perhaps in response to the local community

of prey species. Although clearly beyond the scope of this paper, detailed studies of the prey species and hunting strategies of males and females within each population of sooty owls would be informative.

Stochastic variation is an unlikely explanation for the origin of the leapfrog pattern in the logrunner complex. This is an extremely ancient radiation with levels of interspecific differentiation approaching that typically recorded between avian genera (Avise & Walker 1998). As substantial phenotypic differentiation is expected among taxa of this age, it is the phenotypic similarity between the terminal populations in New Guinea and central-eastern Australia that is anomalous, rather than the distinctiveness of the central form. This implies that the similar phenotypes of *O. novaeguineae* and *O. temminckii* are convergent or pleisiomorphic, but we are unable to distinguish between these alternatives.

5. CONCLUSIONS

While the present study has solved the problem of the origin of the shared leapfrog distribution in sooty owls and logrunners, it also demonstrates the dangers in forming general conclusions from co-distributed species in the absence of molecular data bearing on the histories and phylogenetic relationships of the groups involved. Further insights into the relative roles of vicariance, dispersal and other forces, such as drift and selection, in shaping the Australo-Papuan rainforest biota could come from comparable studies in other genera, with wide disjunctions within and between Australian and New Guinean rainforests, such as the *Zoothera* ground-thrushes, *Arses* monarch-flycatchers, *Ptiloris* rifle-birds, *Cormobates* tree-creepers and *Heteromyias* robins, as well as *Drymodes* scrub-robins found in rainforests and semi-arid habitats.

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REFERENCES

Avise, J. C. & Walker, D. 1998 Pleistocene phylogeographic effects on avian populations and the speciation process. *Proc. R. Soc. Lond.* B **265**, 457–463. (DOI 10.1098/rspb.1998.0317.)

Baird, R. F. 1985 Avian fossils from Quaternary deposits in 'Green Waterhole Cave', south-eastern South Australia. *Rec. Aust. Mus.* **37**, 353–370.

Baird, R. F. 1993 Pleistocene avian fossils from Pyramids Cave (M-89), eastern Victoria, Australia. *Alcheringa* **17**, 383–404.

Boles, W. E. 1993 A logrunner *Orthonyx* (Passeriformes, Orthonychidae) from the Miocene of Riversleigh, northwestern Queensland. *Emu* **93**, 44–49.

Charleston, M. A. 1998 SPECTRUM: spectral analysis of phylogenetic data. *Bioinformatics* **14**, 98–99.

Christidis, L. 1991 Molecular and biochemical evidence for the origins and evolutionary radiations of the Australasian avifauna. In *Proc. 20th Int. Ornithological Congr.* (ed. B. D. Bell, R. O. Cossee, J. E. C. Flux, B. D. Heather, R. A. Hitchmough, C. J. R. Robertson & M. J. Williams), pp. 392–397. Wellington: New Zealand Ornithological Trust Board.

Christidis, L. & Boles, W. E. 1994 *The taxonomy and species of birds of Australia and its territories*. Melbourne, Australia: Royal Australasian Ornithologists Union.

Christidis, L. & Schodde, R. 1991 Relationships of Australo-Papuan songbirds: protein evidence. *Ibis* **133**, 277–285.

Cooke, F. & Buckley, P. A. 1987 *Avian genetics. A population and ecological approach*. London: Academic.

Desjardins, P. & Morais, R. 1990 Sequence and gene organization of the chicken mitochondrial genome. *J. Mol. Biol.* **212**, 599–634.

Diamond, J. M. 1973 Distributional ecology of New Guinea birds. *Science* **179**, 759–769.

Ericson, G. P., Christidis, L., Irestedt, M. & Norman, J. A. 2002 Systematic affinities of the lyrebirds (Passeriformes: *Menura*), with a novel classification of the major groups of passerine birds. *Mol. Phylogenet. Evol.* (In the press.)

Ford, J. 1983 Speciation in the ground-thrush complex *Zoothera dauma* in Australia. *Emu* **83**, 141–151.

Hasegawa, M., Kishino, H. & Yano, T. 1985 Dating of the human–ape splitting by a molecular clock of mitochondrial DNA. *J. Mol. Evol.* **8**, 888–891.

Heidrich, P. & Wink, M. 1994 Tawny owl (*Strix aluco*) and Hume's tawny owl (*Strix butleri*) are distinct species: evidence from nucleotide sequences of the cytochrome *b* gene. *Z. Naturforsch.* **49C**, 230–234.

Heidrich, P., König, C. & Wink, M. 1995 Molecular phylogeny of South American screech owls of the *Otus atricapillus* complex (Aves: Strigidae) inferred from nucleotide sequences of the mitochondrial cytochrome *b* gene. *Z. Naturforsch.* **50C**, 294–302.

Hendy, M. D. & Penny, D. 1993 Spectral analysis of phylogenetic data. *J. Classif.* **10**, 5–24.

Heslewood, M. M., Elphinstone, M. S., Tidemann, S. C. & Baverstock, P. R. 1998 Myoglobin intron variation in the Gouldian finch *Erythrura gouldiae* as assessed by temperature gradient gel electrophoresis. *Electrophoresis* **19**, 142–151.

Joseph, L., Slikas, B., Alpers, D. & Schodde, R. 1999 DNA evidence concerning the identities of *Crax viridirostris* Sclater, 1875, and *C. estudilloi* Allen, 1977. *Ornitologia Neotropical* **10**, 129–144.

Joseph, L., Slikas, B., Alpers, D. & Schodde, R. 2001 Molecular systematics and phylogeography of New Guinean logrunners (Orthonychidae). *Emu* **101**, 273–280.

Kimura, M. 1980 A simple method for estimating evolutionary rates of base substitutions through comparative studies of nucleotide sequences. *J. Mol. Evol.* **16**, 111–120.

Kirchman, J. J., Hackett, S. J., Goodman, S. M. & Bates, J. M. 2001 Phylogeny and systematics of ground rollers (Brachypteraciidae) of Madagascar. *Auk* **188**, 819–863.

Kocher, T. D., Thomas, W. K., Meyer, A., Edwards, S. V., Pääbo, S., Villablanca, F. X. & Wilson, A. C. 1989 Dynamics of mitochondrial evolution in animals: amplification and sequencing with conserved primers. *Proc. Natl Acad. Sci. USA* **86**, 6196–6200.

Lake, J. A. 1987 A rate-independent technique for analysis of nucleic acid sequences: evolutionary parsimony. *Mol. Biol. Evol.* **4**, 167–191.

McGuire, M. 1996 Dialects of the chowchilla *Orthonyx spaldingii* in upland rainforest of north-eastern Australia. *Emu* **96**, 174–180.

Mindell, D. P. & Honeycutt, R. L. 1990 Ribosomal RNA in

vertebrates: evolution and phylogenetic applications. *A. Rev. Ecol. Syst.* **21**, 541–566.

Muse, S. W. & Weir, B. S. 1992 Testing for equality of evolutionary rates. *Genetics* **132**, 269–276.

Norman, J. A., Christidis, L., Westerman, M. & Hill, A. R. 1998 Molecular analysis confirms the species status of the Christmas Island hawk-owl (*Ninox natalis*). *Emu* **98**, 197–208.

Omland, K. E., Tarr, C. L., Boarman, W. I., Martzluff, J. M. & Fleischer, R. C. 2000 Cryptic genetic variation and paraphyly in ravens. *Proc. R. Soc. Lond.* B **267**, 2475–2482. (DOI 10.1098/rspb.2000.1308.)

Remsen, J. V. 1984 High incidence of leapfrog pattern of geographic variation in Andean birds: implications for the speciation process. *Science* **224**, 171–173.

Remsen, J. V. & Graves IV, W. S. 1995 Distribution patterns and zoogeography of *Atlapetes* brush-finches (Emberizinae) of the Andes. *Auk* **112**, 210–224.

Rich, P. V. 1991 The Mesozoic and Tertiary history of birds on the Australian plate. In *Vertebrate palaeontology of Australasia* (ed. P. V. Rich, R. F. Baird, J. M. Monaghan & T. H. Rich), pp. 721–808. Melbourne, Australia: Thomas Nelson.

Saitou, N. & Nei, M. 1987 The neighbor-joining method: a new method for reconstructing phylogenetic trees. *Mol. Biol. Evol.* **4**, 406–425.

Schodde, R. & Calaby, J. H. 1972 The biogeography of the Australo-Papuan bird and mammal faunas in relation to Torres Strait. In *Bridge and barrier: the natural and cultural history of Torres Strait* (ed. D. Walker), pp. 255–300. Canberra: Australian National University Press.

Schodde, R. & Mason, I. 1981 *Nocturnal birds of Australia*. Melbourne, Australia: Landsdowne.

Schodde, R. & Mason, I. 1997 *Zoological catalogue of Australia. 37.2 Aves, Columbidae to Coraciidae*. Melbourne, Australia: CSIRO Publishing.

Schodde, R. & Mason, I. 1999 *The directory of Australian birds. Passerines. A taxonomic and biogeographic atlas of the biodiversity of birds in Australia and its territories*. Melbourne, Australia: CSIRO Publishing.

Swofford, D. 1998 *PAUP* 4.0b8: phylogenetic analysis using parsimony (*and other methods)*. Sunderland, MA: Sinauer.

Tajima, F. & Nei, M. 1984 Estimation of evolutionary distance between nucleotide sequences. *Mol. Biol. Evol.* **1**, 269–285.

Theron, E., Hawkins, K., Bermingham, E., Ricklefs, R. E. & Mundy, N. I. 2001 The molecular basis of an avian plumage polymorphism in the wild: a melanocortin-1-receptor point mutation is perfectly associated with the melanic plumage morph of the bananaquit, *Coereba flaveola*. *Curr. Biol.* **11**, 550–557.

Tobita-Teramoto, T., Jang, G. Y., Kino, K., Salter, D. W., Brumbaugh, J. & Akiyama, T. 2000 Autosomal albino chicken mutation (*ca*/*ca*) deletes hexanucleotide (-deltaGACTGG817) at a copper-binding site of the tyrosinase gene. *Poult. Sci.* **79**, 46–50.

Wu, C.-I. & Li, W.-H. 1985 Evidence for higher rates of nucleotide substitution in rodents than in man. *Proc. Natl Acad. Sci. USA* **82**, 1741–1745.

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